



Environmental forcing of the Campeche cold-water coral province, southern Gulf of Mexico

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Abstract. With an extension of $> 40 \text{ km}^2$ the recently discovered Campeche cold-water coral province located at the northeastern rim of the Campeche Bank in the southern Gulf of Mexico belongs to the largest coherent cold-water coral areas discovered so far. The Campeche province consists of numerous 20–40 m-high elongated coral mounds that are developed in intermediate water depths of 500 to 600 m. The mounds are colonized by a vivid cold-water coral ecosystem that covers the upper flanks and summits. The rich coral community is dominated by the framework-building *Scleractinia Enallopsammia profunda* and *Lophelia pertusa*, while the associated benthic megafauna shows a rather scarce occurrence. The recent environmental setting is characterized by a high surface water production caused by a local upwelling center and a dynamic bottom-water regime comprising vigorous bottom currents, obvious temporal variability, and strong density contrasts, which all together provide optimal conditions for the growth of cold-water corals. This setting – potentially supported by the diel vertical migration of zooplankton in the Campeche area – controls the delivering of food particles to the corals. The Campeche cold-water coral province is, thus, an excellent example highlighting the

importance of the oceanographic setting in securing the food supply for the development of large and vivid cold-water coral ecosystems.

1 Introduction

The last decade has witnessed a tremendous progress in our knowledge about “framework-building cold-water corals” (CWC) as their role as ecosystem engineers creating highly diverse ecosystems in water depths far beyond the shelf edge is becoming more and more obvious (Roberts et al., 2009). The biodiversity associated with these ecosystems may be comparable to that found in tropical coral reefs (Roberts et al., 2006), and they occur almost worldwide except for the highest latitudes (Davies and Guinotte, 2011). The availability of advanced deep-sea technologies (e.g., remotely operated vehicles) greatly supported the discovery and investigation of large, thriving and (so far) unknown CWC ecosystems in remote places. Successful studies such as those performed off Mauritania (Colman et al., 2005), off Angola (Le Guilloux et al., 2009), and in various parts of the Mediterranean

Sea (Freiwald et al., 2009; Orejas et al., 2009; Fink et al., 2013; Gori et al., 2013) demonstrate the potential use of these technologies for future discoveries.

With their rigid carbonate skeletons that can persist over geological timescales CWC shape the sea floor by creating large three-dimensional structures, e.g., > 300 m-high coral carbonate mounds along the Irish margin (e.g., Kenyon et al., 2003; Mienis et al., 2007) reaching back to Pliocene times (~ 2.6 Ma; Kano et al., 2007) and > 100 km²-large reef structures off Norway (Fosså et al., 2005) formed during the Holocene (e.g., López Correa et al., 2012). These structures consist of a mixture of coral skeletons, the skeletal remains of the coral-associated megafaunal community, and pelagic or hemipelagic sediments that can serve as paleoenvironmental archives allowing to reconstruct the long-term development of the CWC ecosystems (e.g., Dorschel et al., 2005; Frank et al., 2009; Titschack et al., 2009; Wienberg et al., 2009; Eisele et al., 2011; Fink et al., 2012; López Correa et al., 2012; Douarin et al., 2013; Thierens et al., 2013).

The scleractinian coral *Lophelia pertusa* is among the most common and most widespread CWC species worldwide and is particularly abundant in the eastern North Atlantic (Davies and Guinotte, 2011). This species withstands a rather wide range of physicochemical conditions (see summary in Davies et al., 2008), a fact that explains its almost global distribution at depths between a few tens of meters to over 2000 m (Freiwald and Roberts, 2005). Another critical factor controlling its distribution is sufficient food supply that is commonly driven by the interplay of surface water productivity and the local nature of the bottom current regime (e.g., currents, stratification, internal waves and tides) delivering food particles to the CWC (Duineveld et al., 2004, 2007; White et al., 2005). Paleoenvironmental studies revealed that food supply often is the decisive factor triggering on- or off-sets of coral growth in a given setting (e.g., Dorschel et al., 2005; Wienberg et al., 2010; Eisele et al., 2011; Fink et al., 2013).

In addition to the CWC hotspot in the eastern North Atlantic, *L. pertusa* also contributes to numerous coral mound structures in the western North Atlantic along the continental margin from North Carolina (Ross and Nizinski, 2007), along the Florida–Hatteras slope (Paull et al., 2010), and The Bahamas to the Florida Straits (e.g., Neumann et al., 1977; Mullins et al., 1981; Grasmueck et al., 2006; Correa et al., 2012a, b). Further west in the Gulf of Mexico, *L. pertusa* appears to be more scattered, forming isolated mound-like structures along the west Florida slope (Newton et al., 1987; Hübscher et al., 2010) and in the northern Gulf of Mexico (Moore and Bullis, 1960; Schroeder, 2002; Reed et al., 2006; Cordes et al., 2008; Becker et al., 2009; Davies et al., 2010). Summarizing the current knowledge, Mienis et al. (2012) conclude that within the Gulf of Mexico CWC mound structures have been rarely found, except on the west Florida slope and in the Viosca Knoll area (Fig. 1). The latter area has been considered the most extensive *Lophelia* habitat found

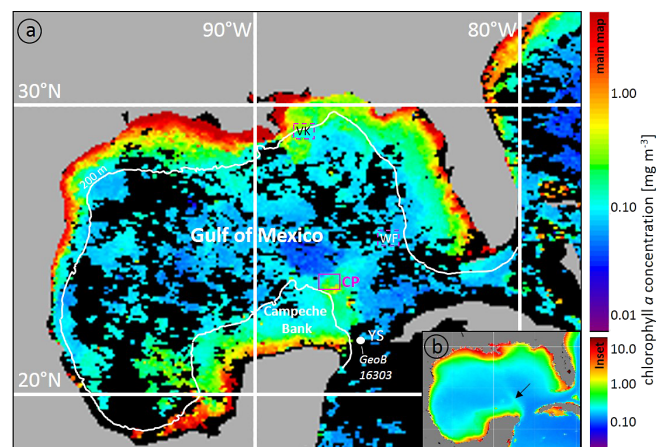


Fig. 1. SEAWIFS satellite ocean color data transferred into chlorophyll *a* concentrations for the Gulf of Mexico (source: <http://oceancolor.gsfc.nasa.gov>). **(a)** The map refers to an 8-day composite representing the period 22–29 September 2010. Black indicates data gaps. The Campeche cold-water coral province (CP) is influenced by increased productivity probably forced by local upwelling at the northeastern rim of the Campeche Bank (Molinari and Morrison, 1988). The white dot in the Yucatan Strait (YS) indicates CTD station GeoB 16303-1. The white line marks the 200 m isobath within the Gulf of Mexico. VK: Viosca Knoll cold-water coral setting (e.g., Brooke and Schroeder, 2007); WF: west Florida cold-water coral mounds (Newton et al., 1987). **(b)** The inset shows the same data as a composite for the entire SEAWIFS mission (4 September 1997 to 30 November 2010). The black arrow indicates the area of the Campeche cold-water coral province that is located in a region marked by a long-term enhanced productivity.

so far in this region (Brooke and Schroeder, 2007; Davies et al., 2010) probably as a consequence of enhanced productivity driven by nutrient-enriched Mississippi River outflow (Wawrik and Paul, 2004). Apart from the Campeche Bank, the southern Gulf of Mexico is generally characterized by meager planktonic biomass along the Mexican slope mirroring the low-productivity Caribbean water that enters the Gulf of Mexico through the Yucatan Strait (Wei et al., 2012).

In this paper, we document for the first time build-ups at the sea floor formed by framework-building scleractinian corals on the slope of the Mexican Campeche Bank, southern Gulf of Mexico. These build-ups are mainly formed by *Enallopsammia profunda*–*Lophelia pertusa* communities. This finding was unexpected as available data from a few dredge haul stations only described the occurrence of the scleractinian CWC *Madrepora oculata* along the margin of the Campeche Bank, north of the Mexican Yucatan Peninsula (Cairns, 1979; Schroeder et al., 2005). Only in 2010 was more detailed information provided, when hydroacoustic surveys revealed “mound-like” structures between 500 and 600 m water depth along the margin of the bank (Hübscher et al., 2010). Without any groundtruthing being available at

that time, it only has been speculated that these structures might be CWC mounds (Hübscher et al., 2010).

This region was revisited in 2012 and extensive field data (bathymetry, hydrography, and video observations) revealed the existence of a large thriving CWC ecosystem, which is the focus of this paper. This hitherto unknown CWC site is here termed the “Campeche CWC province”. The scope of the present study is to describe this extensive ($> 40 \text{ km}^2$) CWC province with respect to morphology, the megafaunal community, and the oceanographic setting and to put it into a larger framework analyzing the overall forcing factors controlling its development.

2 Regional setting

The Campeche Bank is a large shelf area extending approximately 200 km northward from the Mexican Yucatan Peninsula into the Gulf of Mexico (Fig. 1). The Gulf of Mexico is a largely oligotrophic basin with enhanced productivity only along the continental shelves (Müller-Karger et al., 1991), where seasonal coastal upwelling provides additional nutrients to the surface waters (Zavala-Hidalgo et al., 2006). A major source of nutrients is the Mississippi plume fertilizing the northeastern shelves of the Gulf with enhanced productivity partly extending over the continental slope (Wawrik and Paul, 2004). The enhanced productivity triggered by the Mississippi plume most likely plays an important role in sustaining CWC populations along the Louisiana and Florida continental slopes (e.g., Newton et al., 1987; Schroeder, 2002; Fig. 1).

Apart from the typical coastal upwelling, another upwelling regime has been described further offshore along the eastern margin of the Campeche Bank (Merino, 1997). As the curl of the prevailing wind stress is not likely to induce upwelling along the eastern Yucatan slope, the upwelling observed there is probably caused by bottom friction or other topographical effects (Merino, 1997). Nevertheless, the advection of nutrients into the photic zone (although rarely to the sea surface; Merino, 1997) induces very high productivity reaching a peak in September (Zavala-Hidalgo et al., 2006) when sites near the Campeche CWC province appear prominently in satellite-based productivity maps (Fig. 1).

Along its eastern edge the Campeche Bank borders the Yucatan Strait that forms the main passage connecting the Caribbean Sea and the Gulf of Mexico through which the Yucatan Current transports $\sim 24 \text{ Sv}$ from south to north (Sheinbaum et al., 2002). According to Merino (1997) three main water masses comprise the water column there. Salinity and temperature increase together from the Antarctic Intermediate Water (AAIW, 7°C , salinity 34.9) in the deep towards the salinity maximum of the Subtropical Intermediate Water (STUW, 23°C , salinity 36.8) at $\sim 150 \text{ m}$ depth. Further above, temperature rises and salinity declines until from 50 m to the surface both parameters remain relatively constant

($26\text{--}27.5^\circ\text{C}$, salinity < 36.4), representing the Caribbean Surface Water (CSW). At depths greater than $\sim 650 \text{ m}$, the Yucatan and Cuban countercurrents transport water southward while being confined to the western, Mexican side and to the eastern, Cuban side of the Yucatan Strait, respectively (Sheinbaum et al., 2002).

With respect to the strength of the bottom current regime, the best information is provided by mooring data obtained slightly further south in the Yucatan Strait ($\sim 21.5^\circ\text{N}$; e.g., Sheinbaum et al., 2002). Along a W–E transect through the area, the mean northward current velocities at the western margin decrease rapidly from almost 100 cm s^{-1} at the surface to $< 10 \text{ cm s}^{-1}$ at 200 m water depth. However, at the depth of the Campeche CWC province ($\sim 550 \text{ m}$) the bottom current velocities in the Yucatan Strait increase again to $> 10 \text{ cm s}^{-1}$ (Sheinbaum et al., 2002).

3 Methods

All data presented here were collected during expedition MSM 20-4 with the German R/V *Maria S. Merian* in spring 2012 (Hebbeln et al., 2012). They include hydroacoustic measurements, water column studies, and seabed ROV video observation (see Table 1 and Fig. 2 for relevant site information). Instrument specifications and applied settings for the hydroacoustic measurements are described in detail in Hebbeln et al. (2012). For all hydroacoustic measurements introduced below, the essential sound velocity profile through the water column was obtained from two CTD casts in (GeoB 16305-1) and close to (GeoB 16303-1) the working area (Figs. 1 and 2, Table 1).

3.1 Hydroacoustic measurements

3.1.1 Multibeam echosounder (MBES)

Seabed mapping was performed using a KONGSBERG EM1002 multibeam echosounder system (MBES) operating at a frequency of 95 kHz. The EM1002 emitted 111 beams per ping, covered a depth range of 2 to 1000 m and achieved a high depth resolution of 2–8 cm, depending on the pulse length (0.2–2 ms). Achievable swath width on a flat bottom was up to 5 times the water depth dependent on the character of the seafloor. Spatial integrity of the mapping data were achieved by combining the ship's SEAPATH 200 inertial navigation system (INS) including differential global positioning system (DGPS) information with motion data (roll, pitch, heave) provided by the motion reference unit (MRU) 5. The open-source software package MB-System v.5.3.1 (Caress and Chayes, 1996) and the Generic Mapping Tool (GMT) v.4.3.1 (Wessel and Smith, 1998) were used for bathymetric data processing, editing and evaluation. ESRI ArcGIS v.10 was used to create maps (grid cell size: 10 m) and a sustainable spatial data management.

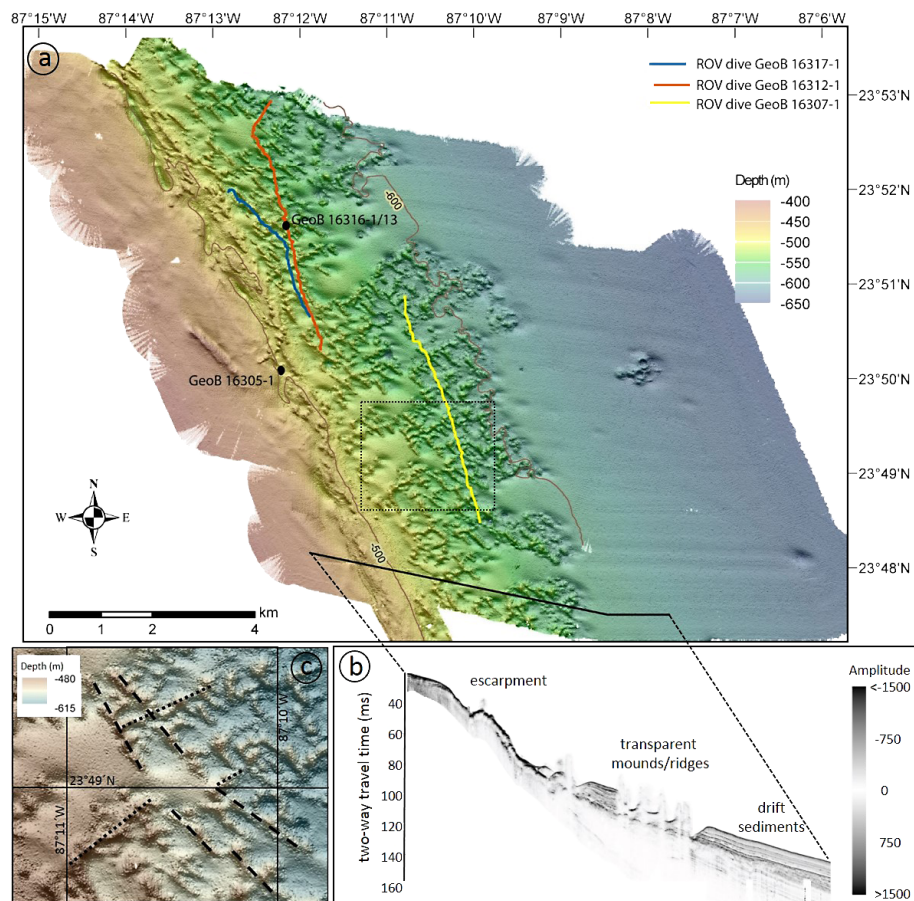


Fig. 2. Overview on the Campeche cold-water coral province (for location see Fig. 1). **(a)** Detailed bathymetric map showing the eastern margin of the Campeche Bank comprising the Campeche cold-water coral province revealing numerous individual elongated coral mounds located mainly between 500 and 600 m water depth. Indicated are CTD sites (black dots) and ROV dive tracks (colored lines; GeoB station numbers are indicated) conducted during R/V *Maria S. Merian* cruise MSM 20-4 (for detailed site information see Table 1). **(b)** PARASOUND profile crossing the slope and highlighting the main morphological units. **(c)** High-resolution view on some of the elongated coral mounds (for position see dotted rectangle in **a**), with the dominant northwesterly directions marked by dashed lines and with the sub-dominant northeasterly directions marked by the dotted lines.

3.1.2 Acoustic Doppler current profiler (ADCP)

Current velocity and direction, and backscatter data through the water column were measured with an RDI Ocean Surveyor acoustic Doppler current profiler (ADCP) operating at a frequency of 75 kHz. Data were acquired using the RDI software VMDAS (Vessel-Mount Data Acquisition) using 128 depth bins of 5 m bin size. Backscatter data were corrected for beam spreading and water absorption (Deines, 1999). For the backscatter data set presented in this study, a constant water absorption coefficient of 0.0272 dB m^{-1} was used (Schulkin and Marsh, 1962). Due to the simultaneous deployment of several hydroacoustic devices, backscatter and current velocity data were affected by acoustic interference, which was removed using appropriate filters. Backscatter data close to the seafloor were biased by side-lobe interferences and not used for interpretation. ADCP data are

presented as a stationary 12 h record collected at site GeoB 16316 (Fig. 2, Table 1).

3.2 ROV video observation and sampling

Three video surveys (GeoB 16307-1, GeoB 16312-1, GeoB 16317-1; Table 1, Fig. 2) were conducted with the ROV *Cherokee* (Sub-Atlantic, Aberdeen, Scotland; operated by MARUM, Bremen, Germany) crossing several CWC mounds along the Campeche margin. The ship-based IXSEA global acoustic positioning system (GAPS) coupled with the ship's DGPS provided an absolute positioning accuracy within 1–2 % of the slant range. The ROV was equipped with a hydraulic manipulator system for sampling purposes, four video cameras including a color video zoom camera for detailed seafloor observation and a digital still camera. The cameras were equipped with two lasers for object size measurements on the seabed; laser scaling was adjusted to

Table 1. Metadata of CTD casts and ROV *Cherokee* video surveys conducted at the Campeche cold-water coral province during R/V *Maria S. Merian* cruise MSM 20-4. Abbreviations: WD: water depth.

Station [GeoB-No.]	Gear		Date [2012]	UTC [hh:mm]	Latitude [N]	Longitude [W]	WD [m]	Remark
16303-1	CTD		21 March	14:59	22° 00.98′	86° 02.95′	1246	Sound velocity profile
16305-1	CTD		22 March	05:21	23° 49.87′	87° 12.27′	506	Sound velocity profile
16316-1 to 16316-13	Yoyo CTD	Start:	24 March	00:20	23° 51.51′	87° 12.12′	576	Hourly casts over ~ 12 h; ADCP data were recorded simultaneously over ~ 13 h
		End:	24 March	12:01	23° 51.52′	87° 12.13′	558	
16307-1	ROV	Start:	22 March	13:51	23° 40.83′	87° 10.03′	547	Video observation
		End:	22 March	16:20	23° 50.49′	87° 10.71′	577	
16312-1	ROV	Start:	23 March	14:31	23° 50.35′	87° 11.76′	523	Video observation
		End:	23 March	18:31	23° 52.52′	87° 12.49′	531	
16317-1	ROV	Start:	24 March	13:37	23° 51.12′	87° 12.53′	555	Video observation
		End:	24 March	15:02	23° 51.77′	87° 12.16′	556	

11.5 cm in a horizontal direction. All video and still-image data were digitally stored. Navigational data (ship, ROV), video recordings, and still images are all time-referenced. With the manipulator of the ROV several coral samples were collected to assess the phenotypes of the different CWC species.

3.3 Water column analyses

To determine the physical parameters of the water masses in the area of the Campeche CWC province and to trace their variability, CTD measurements were performed as a Yoyo CTD comprising 13 individual casts taken within 12 h at station GeoB 16316 (Fig. 2, Table 1). The CTD measurements of the water column down to a maximum water depth of 1246 m were conducted using a SEABIRD “SBE 9 plus” underwater unit and a SEABIRD “SBE 11 plus V2” deck unit. The vertical profile over the water column provided standard data for conductivity, temperature, pressure, and dissolved oxygen. Conductivity and temperature data were used to compute salinity (with the latter being presented here unitless). The data presented here all refer to the downcast of the individual CTD deployments.

4 Results

4.1 Morphology and dimensions of the Campeche cold-water coral province

The hydroacoustic mapping encompasses an area of 180 km² along the northeastern slope of the Campeche Bank and displays three distinct topographical features (Fig. 2). The western part of the map shows an extensive more or less plain area at ~ 440 m water depth. A NNW–SSE orientated and ~ 40 m-high escarpment separates this rather shallow and

plain area from a gently dipping slope to the east, which covers the water depths between 480 and 600 m. Further downslope below ~ 600 m water depth, the slope is followed by a more gently dipping area which comprises smooth sediment of a major drift sediment body (Hübscher et al., 2010). The first 3–5 km of the dipping slope east of the edge are covered by linear and steep-sided elongated mounds between 500 and 600 m water depth. This belt of parallel elongated mounds is situated between the escarpment and the continuous drift deposit, with a few stratified sediment bodies also occurring between the mounds. Both the mounds and the sediment drift overlay a regional truncation surface (Fig. 2b; Hübscher et al., 2010).

The mounds have average heights between 20 and 40 m but can even reach heights of up to 50 m. They vary in length from a few tens of meters to > 1000 m, and trend in two directions. The dominant direction is NW–SE and the second one NE–SW (Fig. 2c). In many cases both directions merge, thereby forming V-shaped elongated mounds pointing with the tip to the WNW. ROV-based video observations reveal that the morphology of these mounds is mostly rather steep with estimated angles of up to 30° (e.g., Fig. 3e). These elongated mounds are often aligned by a moat towards the next mound (Fig. 2). In addition, on some of the mound flanks exhumed carbonate crusts with irregular upper and lower surfaces have been observed (Fig. 3h). As the video observations clearly indicate that these mounds are covered by a vivid CWC ecosystem (Figs. 3a, b and 4a, b), the entire structure is termed here the Campeche CWC province. The minimum extension of the Campeche CWC province is 40 km²; however, most likely this CWC province is even larger, as it still has a significant width at the northern and southern boundaries of the mapped area (Fig. 2). Thus, the ultimate northern and southern boundaries of the Campeche CWC province still need to be verified.

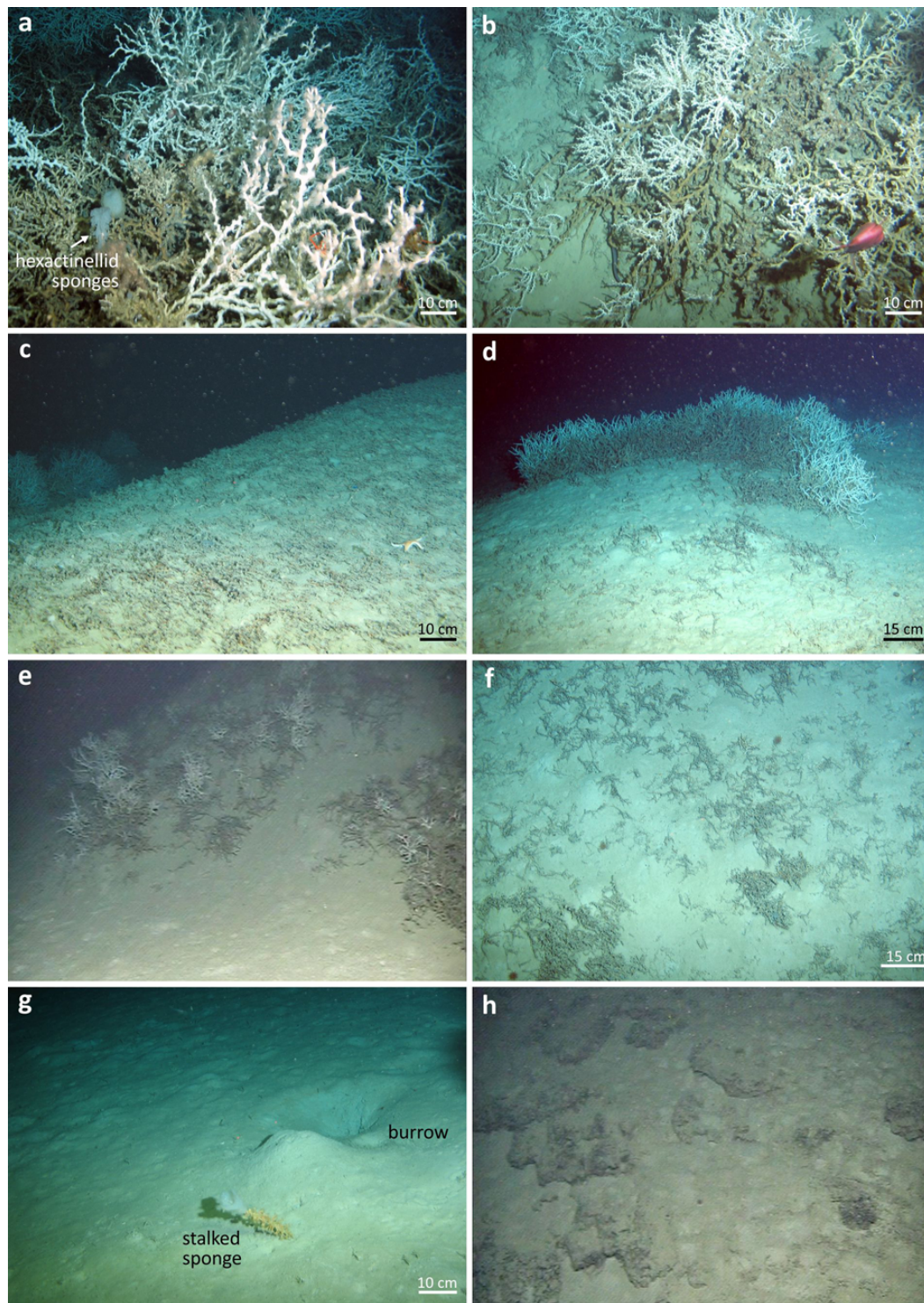


Fig. 3. ROV images showing the variety of facies types observed for the Campeche cold-water coral province (images copyright MARUM, Bremen, ROV *Cherokee* team). **(a)** Coral mound summit: dense colonies of *Lophelia pertusa* – note Hexactinellid sponges (*Aphrocallistes* sp.) and squat lobster; **(b)** current-exposed coral mound flank: ensemble of the fragile *Enallopsammia profunda* and the brachycephala morphotype of *L. pertusa*; **(c)** mound flank packed with dead coral framework; **(d)** arcuate *E. profunda* thicket on a low-relief mound; **(e)** sudden facies change from flat soft sediment plain to steeply inclined coral mound flank; **(f)** lower coral mound flank: dispersed fragments of *E. profunda*; **(g)** intermound area: strongly bioturbated soft sediment – note stalked sponge (*Hyalonema* sp.) colonized by actinarians; and **(h)** occasionally observed outcropping carbonate crusts.

4.2 The Campeche cold-water coral ecosystem

Observations during three ROV dives that cross several mounds of the Campeche CWC province reveal the composition of the structure-forming CWC and their associated megafaunal community. The dive tracks of the video surveys had an NNW–SSE orientation in water depths ranging 510–580 m (Fig. 2). All mounds studied are colonized by colonial scleractinians representing *Enallopsammia profunda*–*Lophelia pertusa* communities (Figs. 3 and 4), whereas the flat seabed between the mounds consists of pelagic unconsolidated mud enriched by globigerinid foraminifers and thecosomatous gastropods, locally admixed with patches of coral rubble and mollusk shell hash (see detailed description of collected sediment samples in Hebbeln et al. (2012)). These intermound areas are strongly bioturbated as indicated by widespread lebensspuren and burrows (Fig. 3g).

Coral colonization, coral density and coral species distribution show a clear zonation related to current exposure and position on the mound flank. In general, living corals occur at the highest parts of the mounds, followed downslope by a zone of coral rubble and by plain soft sediments in the lower parts of the mounds and in the areas between the mounds (Fig. 3). However, on some steeply inclined mounds (up to 30°), coral colonization starts already at the base of their current-exposed side (SSE), thereby generating a sharp change of sedimentary facies from pelagic muds to a living CWC ecosystem. On less steep mounds live coral colonies start to appear halfway upslope the current-exposed flank, or the mound flanks are entirely covered by a dead and collapsed coral framework or coral rubble with only few live coral colonies in between. For both types of mounds, corals fade off halfway along the leeward flanks of the mounds. Overall, the density of coral framework and the proportion of live coral colonies become progressively higher towards the summit, where they can form very dense coral thickets up to 60 cm thick. The mound flanks are dominated by *E. profunda*, whereas *L. pertusa* becomes increasingly abundant, if not dominant on the summits.

The dendroid *E. profunda* colonies display an open-spaced growth habit with individual colony branches pointing in all directions (Fig. 4a and b). This growth habit results in a loose mesh of coral framework, thus facilitating framework disintegration of individual branches into stick-like fragments. Colony heights vary from 20 to 60 cm; thus only the upper 10–15 cm of a colony yields live coral polyps and translucent tissue. *Lophelia pertusa* also constructs an open-spaced coral framework. However, secondary fusion between adjacent coral branches is a very common feature, thus increasing the structural integrity of the entire framework considerably in comparison to *E. profunda*. The branches of *L. pertusa* are strongly calcified and slender with individual corallite lengths of 2.5–3.5 cm and calicular diameters of 0.5–0.8 cm. This phenotype has been described as forma *gracilis* by Duncan (1873) and is in contrast to the stout

branches with extremely wide calicular diameters of the *brachycephala* form (Fig. 4a) described by Moseley (1881) and Cairns (1979). The latter phenotype occurs in low numbers in the Campeche CWC province, but the co-occurrence of the two *L. pertusa* growth forms is a well-known phenomenon in the northern Gulf of Mexico (Newton et al., 1987; Brooke et al., 2009). The *Lophelia* framework can attain heights of 50 cm, and the zone of live polyps and translucent tissue coverage stretch over a range of 20–30 cm.

The live coral zone is utilized by the associated community in various ways and differs largely in terms of species composition and richness from the associated community found in the tissue-barren, exposed coral framework beneath. Common organisms observed (although not exclusively) in the live zone are the predatory decapods *Bathynectes longispina*, *Eumunida picta*, *Chaceon fenneri*, *Munidopsis* sp. and *Rochinia crassa* and the grazing echinoids *Cidaris* sp. and *Gracilechinus* sp. (Fig. 4e). The latter echinoid has been recognized as a corallivore in CWC habitats of the eastern North Atlantic (Stevenson and Rocha, 2013). Other organisms with corallivore affinities in the live coral zone are star fishes of the genus *Hippasteria* (Mah et al., 2010) and the muricid gastropod *Coralliophila richardi* (Taviani et al., 2009), which were commonly collected from the live coral zone. Stalkless crinoids have been occasionally observed to take advantage of the elevated and current-exposed position of live coral branches for filtering particles from the water. Indication of probably necrotic epibiosis of live scleractinians by zoanthids and actinarians in some scleractinian colonies is a common feature and seems to cause local mortality. Polychaetes of the genus *Eunice*, from which several species are known as symbionts of *L. pertusa* and other colonial CWC (e.g., Buhl-Mortensen and Mortensen, 2004; Mueller et al., 2013), are surprisingly rare in the Campeche CWC province.

Characteristic organisms of the tissue-barren, exposed coral framework are flytrap anemones (probably *Actinoscyphia* sp.; Fig. 4b), isidid corals (*Keratoisis* sp.), and solitary scleractinians (*Desmophyllum dianthus*, *Javania cailetti*, *Stenocyathus vermiformis*, *Trochopsammia infundibulum*). The glass sponge *Aphrocallistes* sp. was found attached to the coral framework. Apparently the glass sponges are living together with masses of yellow actinarians (Fig. 4f), thus resembling the recently described symbiotic relationship between the glass sponge *Hyalonema sieboldi* with the actinarian *Spongiactis japonica* (Sanamyan et al., 2012). Common fishes encountered frequently in the coral framework were *Helicolenus dactylopterus* and *Nettenchelys exoria*. Gorgonians and antipatharians that are elsewhere common in CWC ecosystems are extremely rare here.

The coral rubble is strongly admixed with unconsolidated pelagic mud, thereby providing small hard-substrate islands within soft sediment. Common megafaunal organisms are large astrorhizid foraminifers, cerianthids, pennatulaceans, stalked glass sponges (*Hyalonema* sp.), and the

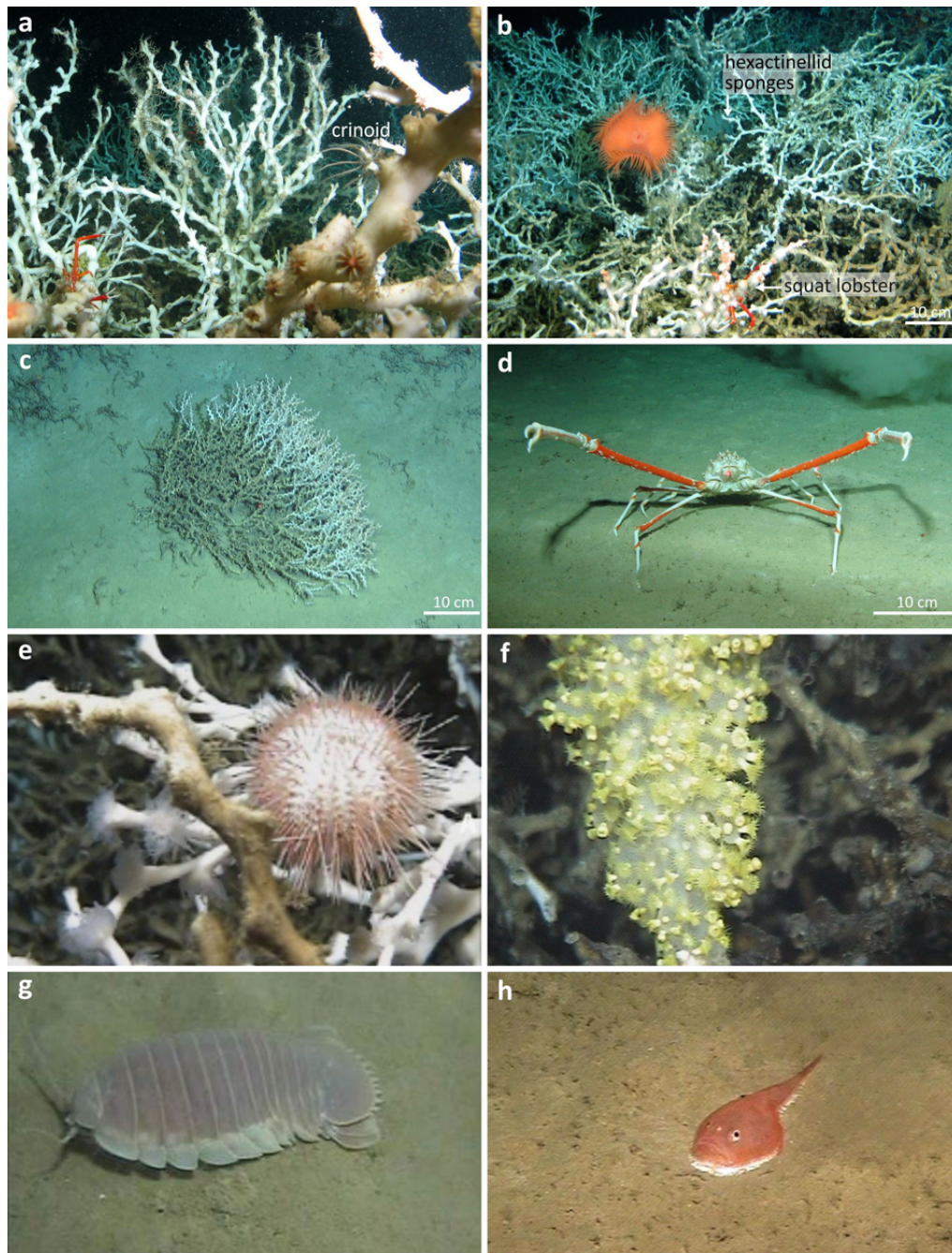


Fig. 4. ROV images showing examples for the megafaunal community present in the Campeche cold-water coral province (images copyright MARUM, Bremen, ROV *Cherokee* team). (a) Dense colonization of *Lophelia pertusa* at the coral mound top; (b) flytrap anemone (probably *Actinoscyphia* sp.) colonizing tissue-barren, exposed coral framework; (c) displaced but still alive colony of *Enallopsammia profunda*; (d) brachyuran crab *Rochinia crassa*; (e) grazing of living corals by the echinoid *Gracilechinus* sp.; (f) glass sponge *Aphrocallistes* sp. living together with masses of yellow actinarians; (g) the giant cirrolanid isopod *Bathynomus giganteus*; and (h) the anglerfish *Chaunax suttkusi* commonly spotted near the coral mounds resting on the seabed.

common decapods (same as in the live zone) and shrimps. Amongst the mobile organisms, the giant isopod crustacean *Bathynomus giganteus* was detected (Fig. 4g). Like in other coral rubble habitats elsewhere in the Gulf of Mexico and

in the northern North Atlantic, the anglerfish *Chaunax suttkusi* (Fig. 4h), was commonly spotted near the coral mounds resting on the seabed (Caruso et al., 2007). Other common fishes observed in the coral rubble and pelagic mud areas

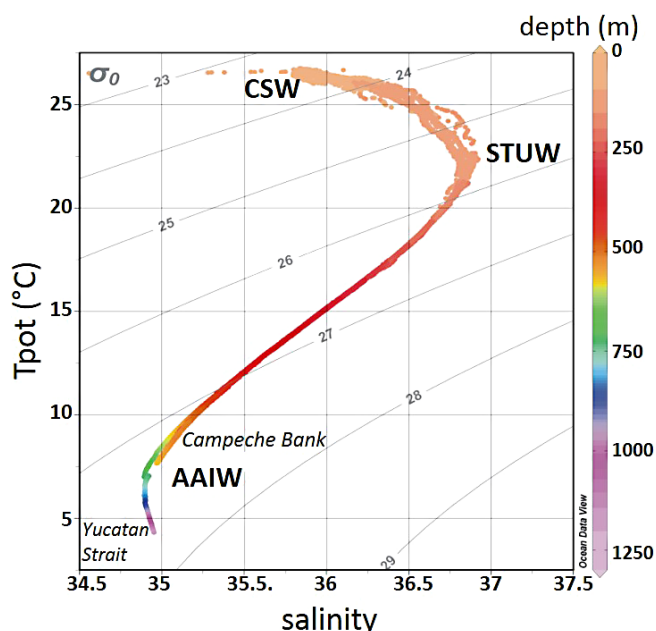


Fig. 5. Water mass structure in the Yucatan Strait (GeoB 16303-1) and in the Campeche cold-water coral province (GeoB 16316-1 to -16, Yoyo CTD station; see Table 1). Shown is a temperature–salinity plot; temperature is displayed as potential temperature (T_{pot}), grey lines indicate levels of isodensity (σ_θ) in kg m^{-3} (plotted using Ocean Data View v.4.5.1; <http://odv.awi.de>; Schlitzer, 2012). Abbreviations: CSW: Caribbean Surface Water; STUW: Subtropical Intermediate Water; AAIW: Antarctic Intermediate Water.

are *Chlorophthalmus agassizi*, *Laemonema* sp., *Nezumia* sp., Phycidae and Rajidae.

4.3 Water column structure/dynamics

The CTD measurements allow the identification of the most important regional water masses, based on temperature (potential temperature) and mainly on salinity data (Fig. 5). The uppermost ~ 80 m of the water column are characterized by water with salinities of < 36.4 , which is indicative of the presence of the CSW. The salinity maximum (~ 36.8) between 100 and 160 m water depth is characteristic for the STUW. At 540 m water depth salinity drops below 35.0, marking the presence of AAIW. In the depth range where living CWC have been observed (520 to 580 m) temperatures range 7.5 – 9.5 °C and salinities 34.9 – 35.1 . Dissolved oxygen contents vary between 2.74 and 2.8 mL L^{-1} .

The Yoyo CTD station (GeoB 16316) consisting of 13 individual, hourly taken casts reveal small but significant variations also in the deepest part of the water column just above the Campeche CWC province (Fig. 6): for example, at 519 m water depth the temperature varies by almost 1 °C up to three times over the 12 h measuring period (Fig. 6c). These temperature changes are also reflected in the depth position of individual isotherms (8 to 9.5 °C, Fig. 6b). They fluctuate

vertically by up to 20 m, thereby reflecting the same temporal forcing as the temperatures at 519 m depth. Along with these temperature changes a distinct density gradient induced by temperature and salinity changes, almost reaching 0.7 °C and 0.07 , respectively, over a 10 m depth interval (Fig. 6d) propagates across the site. With ~ 0.06 kg m^{-3} per 10 m depth interval this density gradient is strongest for the lower part of the water column at 525 m depth and significantly higher than the density gradients between 380 m and the sea floor that otherwise reach maximum values of ~ 0.04 kg m^{-3} per 10 m depth interval (Fig. 6a).

The ADCP data collected over a 13 h time interval (simultaneously to the Yoyo CTD data; see Table 1) allow distinguishing between three major layers that show some internal (although less pronounced) horizontal structuring (Figs. 7 and 8). Within the upper 130 m of the water column, the highest current velocities (74 – 83 cm s^{-1}) occur together with a high backscatter (94 – 98 dB). Current directions vary between 322° and 335° . The second layer between 130 and 460 m is characterized by continuously decreasing current velocities from 63 to 42 cm s^{-1} , again by rather stable current directions similar to the uppermost layer (325° to 336°), and by low backscatter values (84 – 94 dB). The bottom layer (> 460 m) is marked by a significant change in current direction (343° to 360°) and by the lowest but still strong currents flowing at a rate of 24 to 42 cm s^{-1} .

At the beginning of the stationary ADCP record (ca. 00:00 UTC, 24 March 2012) enhanced backscatter signals move upward through the water column towards the sea surface. By the end (ca. 11:30 UTC), similar signals move downward towards the seabed (Fig. 7). Similar observations were made during additional ADCP surveys in the working area during cruise MSM 20-4 (Hebbeln et al., unpublished data). In total, four upward (always at around 0:00 UTC, corresponding to 18:15 local “solar” time at 86° W, i.e., sunset) and two downward movements (always at around 11:30 UTC, corresponding 05:45 local solar time at 86° W, i.e., sunrise) were observed.

5 Discussion

Large CWC-formed seafloor structures have been reported from many regions in the world’s oceans (see compilation in Freiwald and Roberts (2005)). In addition to the > 300 m-high CWC mounds off Ireland (Kenyon et al., 2003; Mienis et al., 2007; Dorschel et al., 2010), the extensive reefs off Norway (e.g., Fosså et al., 2005) are the most impressive features. Extending over tens of kilometers (e.g., the Sula Reef, $\sim 14 \times 0.5$ km, Freiwald et al., 2002; the Røst Reef, $\sim 40 \times 3$ km, Fosså et al., 2005) and reaching up to ~ 40 m in height, these reefs generally comprise clusters of individual frameworks rather than a single coalescent structure (Freiwald et al., 2002). The Campeche CWC province shows a similar appearance as it comprises a cluster of individual

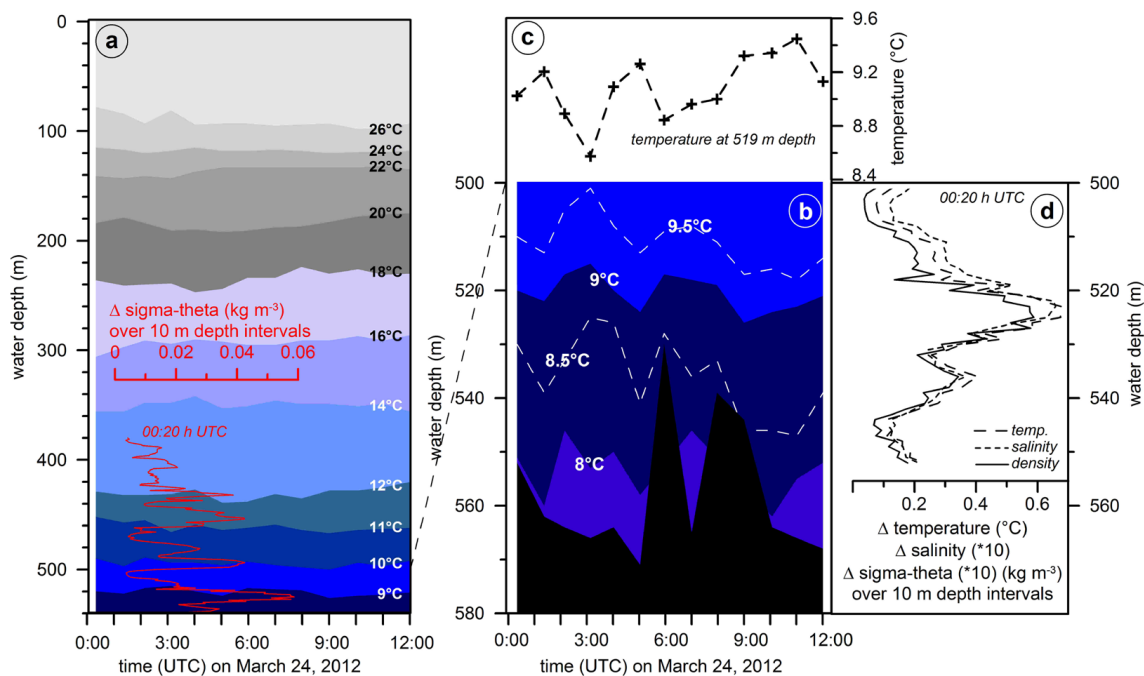


Fig. 6. Hydrological variability derived from the Yoyo CTD station GeoB 16316 (see also Table 1 and Fig. 1). **(a)** Variability of the temperature distribution in the entire water column over a time interval of 12 h (comprising 13 individual CTD casts). The red inset shows the density gradient over 10 m depth intervals for the water column below 380 m taken from CTD cast GeoB 16316-1 (00:20 UTC). **(b)** Depth variation of the 8 °C to 9.5 °C isotherms in the lower part of the water column > 500 m water depth over the same time period shows partly vertical movements of > 20 m. Variations in water depth (black denotes the sea floor) are caused by slight movements of the vessel (~ 600 m N–S, ~ 50 m E–W) at the Yoyo CTD station (including the crossing of a CWC mound). **(c)** Water temperature at 519 m depth measured over the same time period indicates a variability of up to 1 °C. **(d)** Gradients in temperature, salinity, and density over 10 m depth intervals. Data were obtained during the individual CTD cast GeoB 16316-1 (00:20 UTC) and reveal particularly strong gradients around 520 m water depth (see also a).

elongated coral mounds rather than a single clearly confined reef structure. The term “province” is used for the present study to describe the CWC mounds along the Campeche Bank following the nomenclature developed for the Irish margin where numerous individual CWC mounds occur clustered in provinces (e.g., White and Dorschel, 2010). With its mapped area of 10 × 4 km, and most likely further northwest- and southeastward extensions, the Campeche CWC province is comparable with the large Norwegian reefs and, thus, belongs to the largest mapped CWC provinces in the world. In addition, the Campeche CWC province represents the most important and extensive flourishing azooxanthellate coral area in the entire Gulf of Mexico discovered so far. The geographically closest CWC province is situated along the Miami Terrace in the Straits of Florida, where 27 km² of elongated coral mounds are mapped in detail by an autonomous underwater vehicle (Correa et al., 2012a) in an area where earlier studies have reported occurrences of “muddy mounds” and “sand ridges” (Neumann and Ball, 1970).

Whereas the large Irish coral mounds have been accumulated over > 2 million years (Kano et al., 2007), the Norwegian reefs have been formed only during the last

~ 10 000 years of the Holocene (e.g., López Correa et al., 2012), when during the last deglaciation the Fennoscandian Ice Sheet retreated beyond the present-day coastline. Large seafloor structures formed by CWC cannot easily be transferred into age, as, for example, the Irish mounds at some point in time changed from a distinct accumulation stage into an almost stagnation stage marked by CWC growth and sediment deposition alternating with extensive periods dominated by erosion (Dorschel et al., 2005; Kano et al., 2007; Eisele et al., 2008). Thus, the average height of the Campeche coral mounds of 20 to 40 m does not allow for estimating the onset of coral growth in the region. Nevertheless, their size and the collection of a > 10 m-long sediment core containing abundant coral fragments embedded in a matrix of hemipelagic sediments (Hebbeln et al., 2012) reveal that also the Campeche CWC ecosystem has a relevant, although yet not constrained, history.

This sedimentary record adds to the PARASOUND evidence for a “CWC origin” of these mounds. The coral mounds show little to no internal layering and are often transparent (Fig. 2b), which is a common feature for coral carbonate mounds (e.g., Van Rooij et al., 2003; Savini et al.,

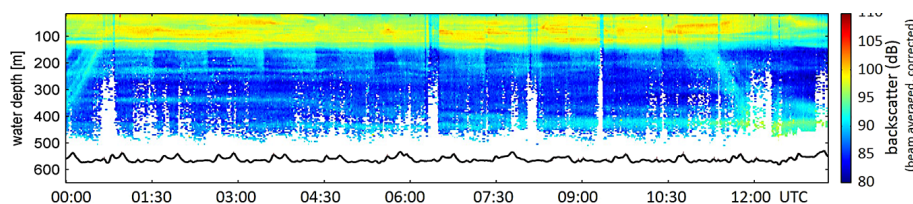


Fig. 7. ADCP-derived backscatter data obtained during a 13 h stationary measurement from 00:00 to 13:00 UTC on 24 March 2012. ADCP data were recorded simultaneously to the Yoyo CTD station GeoB 16316 (see Table 1). This backscatter record shows the upward (0:00–0:30 UTC, local sunset) and downward (11:30–12:00 UTC, local sunrise) migration of the zooplankton. Probably biased data close to the seafloor have been omitted.

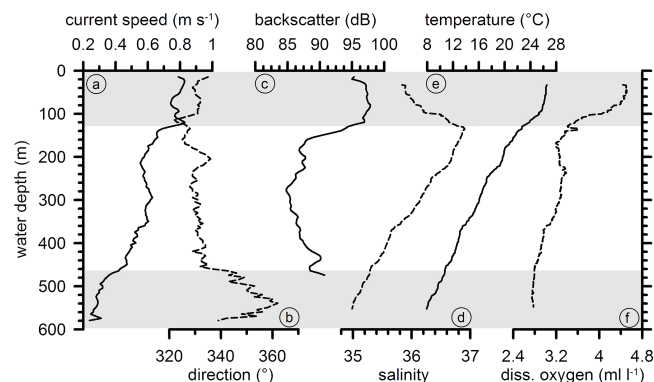


Fig. 8. Water column data for the Yoyo CTD site GeoB 16316. Mean values for (a) current speed, (b) current direction, and (c) backscatter averaged from the 13 h stationary ADCP measurement. CTD data from cast GeoB 16316-1 for (d) salinity, (e) temperature, and (f) dissolved oxygen. The dashed lines refer to the lower x axes. The grey shadings delineate the different layers of the water column as derived from the ADCP data.

2014). The PARASOUND profile crossing the Campeche CWC province from west to east displays a strong reflection underneath the drift sediment bodies and the CWC mounds developed along the Campeche Bank slope (Hübscher et al., 2010). It is assumed that this continuous strong reflector forms the base of the coral mounds (Hübscher et al., 2010) that might have provided the hardground allowing for the initial coral settlement similar to the erosional unconformity forming the base of the Irish CWC mounds (Van Rooij et al., 2003; Kano et al., 2007).

CWC often form coral mounds that can have a variety of shapes, from circular to elongate (Roberts et al., 2009). Elongated mounds often have been related to the presence of an unidirectional bottom current regime, however, with elongated coral mounds sometimes occurring perpendicular (Correa et al., 2012a) and sometimes parallel (Messing et al., 1990) to the main current direction. The elongated coral mounds within the Campeche CWC province appear to be generally aligned parallel to the main current direction possibly following an upstream growth pattern as outlined by Messing et al. (1990). They mostly stretch towards 330° with

some heading towards 300° (with a second-order direction NE–SW; see above). These directions are close to the two main current directions of 330° (above ~ 470 m) and 360° (below ~ 470 m) derived from the ADCP data (Fig. 8) which, however, only represent a snapshot in time. Temporal variations (e.g., lunar, seasonal) below 470 m might result in the different directions of the coral mounds observed. Then, the 30° offset between both current directions and both mound directions observed could speculatively be related to an inherent 30° relationship between coral mound extension and prevailing current direction.

5.1 The Campeche cold-water corals and associated community

The Campeche CWC province is constructed by *Enallopsammia profunda* and to a lesser degree by *Lophelia pertusa*. Neither of the scleractinians have been reported in previous publications from the Campeche slope (e.g., Cairns, 1979; Cairns et al., 1993) but are known from several locations in the Caribbean Sea and northern Gulf of Mexico (see compilations of published and unpublished information by Brooke and Schroeder, 2007; Lutz and Ginsburg, 2007; Messing et al., 2008). While *L. pertusa* has a nearly cosmopolitan distribution, *E. profunda* is endemic to the western Atlantic from the Antilles in the south to off Massachusetts in the north at water depths of 146–1748 m (Cairns, 1979). Structure-forming *Enallopsammia*–*Lophelia* frameworks are known from the base of the Florida–Hatteras slope in 500–800 m water depth and from Miami to South Carolina (Reed, 2002). Correa et al. (2012a) describe an approximately 20 km² field of *Enallopsammia*–*Lophelia* coral mounds at the base of the Miami Terrace, Straits of Florida, at 630–870 m depth, with a denser coral framework on current-facing flanks and summits. The same coral association is present in the CWC mound province at the toe of the Great Bahama Bank (Correa et al., 2012b). Interestingly, on the ROV tracks studied only a low abundance of associated megafauna in the Campeche CWC province was documented. This is in contrast to other scleractinian coral framework habitats in the northern Gulf of Mexico (Lessard-Pilon et al., 2010) or in the eastern North Atlantic (e.g., Henry and Roberts, 2007; Roberts et al., 2006). For instance, with the exception of

Aphrocallistes sp. and a few *Keratoisis* sp., no other large suspension-feeding megabenthos were observed during the three ROV dives. It should be kept in mind that the visually inspected portion of the Campeche coral province is far too small for a solid conclusion at present and further inspections may change this first impression considerably.

Regarding the structure-forming CWC from the Campeche Bank on a wider perspective, this newly found CWC province is located at a key position, namely at the beginning of the Loop Current that passes over the well-known CWC occurrences of Louisiana and west Florida before it becomes the Florida Current flowing through the Straits of Florida. North of the Straits of Florida the Florida Current forms 90 % of the Gulf Stream, passing north along the margins of South Carolina and Georgia, from where also large CWC provinces have been reported (Ross, 2007; Ross and Quattrini, 2007; Messing et al., 2008). South of the Campeche CWC province, *Lophelia* is known from off Brazil, Venezuela and Colombia and was recently mapped off Roatan, Honduras (Reyes et al., 2005; Lutz and Ginsburg, 2007; Arantes et al., 2009; Mangini et al., 2010; Etnoyer et al., 2011), thus following the path of the northward-flowing AAIW that bypasses the Campeche Bank (Merino, 1997). Such an oceanic intermediate water gateway (sensu Henry, 2011) may exert strong control on coral larval dispersal routes as has been documented for *Desmophyllum dianthus* populations in the South Pacific (Miller et al., 2011).

5.2 Environmental control on the Campeche cold-water coral ecosystem

The known ranges of temperature (4–13.9 °C; Roberts et al., 2006; Freiwald et al., 2009), salinity (31.7–38.8; Freiwald et al., 2004; Davies et al., 2008), dissolved oxygen (2.7–7.2 mL L⁻¹; Dodds et al., 2007; Davies et al., 2008; Davies et al., 2010) and other physicochemical parameters defining the ecological niche of *L. pertusa* in the eastern North Atlantic (see summary in Davies et al., 2008) are found in many parts of the world's oceans (Davies and Guinotte, 2011). Water mass properties obtained for the Campeche margin, such as temperature (9.5–7.5 °C) and salinity (35.1–34.9), fit well into these defined thresholds (Fig. 7). The observed content of dissolved oxygen of ~2.7 mL L⁻¹ matches observations from the Viosca Knoll area in the northern Gulf of Mexico, where *Lophelia* colonies currently thrive at the lowest reported oxygen levels of 2.7–2.8 mL L⁻¹ (Davies et al., 2010). It is assumed that these extreme oxygen conditions cause decreased growth rates or even inhibit reproductive processes (Brooke and Young, 2003).

However, despite a suited physicochemical setting, the presence of suitable hardgrounds for the corals to settle on, and even more importantly the availability of sufficient food, is crucial for the establishment and long-lasting development of a vivid CWC ecosystem. In general CWC feed on fresh phytodetritus (Duineveld et al., 2004; Kiriakoulakis et al.,

2005; Duineveld et al., 2007), on zooplankton (Carlier et al., 2009; Dodds et al., 2009) or on a combination of both (Becker et al., 2009; van Oevelen et al., 2009). Recent laboratory studies also revealed the importance of dissolved organic matter which might be actively absorbed by CWC especially during periods when particulate food is scarce (Gori et al., in press). However, independent of the food source, the sessile CWC rely on sufficient food supply, which is based on primary production in the surface waters and the delivery of food particles to the CWC living at intermediate depths. For the latter, various mechanisms were identified to enhance and transport food particles to the CWC, including strong bottom currents, downwelling and cascading, internal tides and waves, and nepheloid layers which act as a pathway for lateral transport (White et al., 2005; Dorschel et al., 2007; Duineveld et al., 2007; Mienis et al., 2007; Davies et al., 2009; Orejas et al., 2009). On the local to regional scale, topography also influences hydrodynamic processes, as, e.g., internal waves, down- or upwelling. Thus, for any given location it is the interplay of all these factors allowing for or prohibiting the presence of CWC.

For the Campeche CWC province, the provision of food to the CWC appears to be almost optimal, and therefore the observed paucity of the coral-associated megafauna remains to be explained. Primary productivity in the surface waters is high (up to ~1 mg Chl *a* m⁻³; Fig. 1) due to the local upwelling center that is located just above the Campeche CWC province (Merino, 1997). Current meter data from the Yucatan Strait (Sheinbaum et al., 2002) as well as the ADCP data collected during cruise MSM 20-4 reveal reasonably strong bottom currents with average velocities of ~30 cm s⁻¹ between 500 and 600 m water depth (Fig. 8). These numbers are in line with in situ current measurements at other CWC sites indicating maximum velocities of > 50 cm s⁻¹ (Dorschel et al., 2007; Mienis et al., 2007), whereas average current velocities can be as low as 8 cm s⁻¹ (Mienis et al., 2007).

Furthermore, the strong density gradient undulating around 520 m (Fig. 6d) might act as a decelerator for sinking (food) particles, thereby prolonging their residence time within the reach of the CWC and, thus, enhancing the probability of these particles to be caught by the corals. With salinities varying around 35, this density gradient possibly marks the upper limit of the core of the AAIW. A similar mechanism has been suggested to support the CWC off Ireland, there benefitting from the density gradient developed at the upper limit of the Mediterranean Outflow Water (White and Dorschel, 2010). For the northeastern North Atlantic, Dullo et al. (2008) described a narrow potential density envelope of sigma-theta (σ_θ) = 27.35–27.65 kg m⁻³ preferred by the CWC. Along the Campeche Bank the density of the water masses surrounding the CWC is slightly lower, at 27.18–27.29 kg m⁻³, and, thus, close to data reported from the Viosca Knoll area (27.1–27.2 kg m⁻³) (Davies et al., 2010). In contrast, living CWC settings in the Mediterranean Sea are

associated with much higher densities of $> 29 \text{ kg m}^{-3}$. Thus, if applicable, the concept of a narrow density envelope defining the overall habitat range of the CWC as suggested by Dullo et al. (2008) needs to be regionalized (see also Flögel et al., in press). However, the obvious steep gradient in density (Fig. 6d) seems to be a sensitive indicator for living CWC reef communities.

As indicated by the undulating isotherms (Fig. 6), the temporal variability of the local hydrographic setting, which might reflect the presence of internal waves, literally might pump the food particles through the CWC ecosystem, especially those particles temporarily accumulating along the strong density gradient, as suggested by Mienis et al. (2012). Over the observed 13 h, the depth range covered by the fluctuating maximum near-bottom density gradient aligns with the upper range of observed living CWC in $\sim 515\text{--}530 \text{ m}$ water depth. Assuming a larger variability associated with monthly (i.e., lunar) to seasonal forcing, one may speculate that the entire depth range of living CWC off the Campeche Bank might intermittently be affected by such a pumping process. Due to the limited length of the 13 h of observation no tidal signal providing additional energy to the bottom current regime could have been clearly detected. However, along the mooring transect across the Yucatan Strait mentioned before (Sheinbaum et al., 2002), a comparably high amplitude of the major axis of the dominant diurnal O_1 tide was observed exactly in the depth range of the Campeche CWC province (Carrillo González et al., 2007).

The ADCP data also point to another possible food source for the corals. The strong upward-rising backscatter signal at dusk and the down-going signal at dawn (Fig. 7) are indicative of the diel vertical migration of zooplankton (Heywood, 1996). According to the backscatter data shown in Fig. 7 the migrating zooplankton spend the day at depths of $> 300 \text{ m}$, with any deeper-reaching migration being obscured by bottom interferences of the backscatter signal. In case the zooplankton actively descend to the depths of the CWC, it might serve as an additional process enhancing the delivery of food to the CWC. The depth range of the Campeche CWC is often reached by migrating zooplankton. For instance, off the California coast, a depth of $\sim 560 \text{ m}$ has been shown to be a preferred depth of the zooplankton at which to spend the daytime (Plüddemann and Pinkel, 1989). The potential of daily migrating zooplankton as an additional food source for the CWC has also been put forward by Mienis et al. (2012) based on ADCP observations in the Viosca Knoll area in the northern Gulf of Mexico.

6 Conclusions

The Campeche CWC province is one of the largest coherent CWC areas discovered so far, and the most relevant in the western Atlantic Ocean. A healthy and highly diverse CWC ecosystem is developed on top of a complex system

of 20–40 m-high, partly interconnected elongated mounds, which probably can serve as a paleoenvironmental archive enabling the reconstruction of the long-term development of the Campeche CWC province over the Late Quaternary climatic cycles.

The location of the Campeche CWC province appears to be almost perfect for the establishment of such a large CWC ecosystem. It is (a) located underneath a local upwelling center providing high primary production, (b) influenced by a very dynamic bottom current regime delivering food particles to the corals, and (c) characterized by a physicochemical setting that fits the recognized ecological needs of *L. pertusa*. The observed diel vertical migration of zooplankton possibly reaching the intermediate depth of the CWC ecosystem may even serve as a supplemental food source as already indicated by Mienis et al. (2012). These observations fits several paleoenvironmental studies, highlighting the controlling role of the food supply on the long-term development of such ecosystems (Dorschel et al., 2005; Wienberg et al., 2010; Eisele et al., 2011; Fink et al., 2013).

In many places in the world's oceans the physicochemical setting comply with the niche requirements of *L. pertusa* and other CWC (Davies and Guinotte, 2011); however, only in some of these places have CWC ecosystems developed. Thus, the Campeche CWC province appears to be an excellent example showing that food supply – controlled by a variety of mechanisms – plays a major role in the development of CWC ecosystems.

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